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The role of attention in motion extrapolation: Are moving objects ‘corrected’ or flashed objects attentionally delayed?

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Abstract. Objects flashed in alignment with moving objects appear to lag behind [Nijhawan, 1994 *Nature (London)* **370** 256–257]. Could this ‘flash-lag’ effect be due to attentional delays in bringing flashed items to perceptual awareness [Titchener, 1908/1973 *Lectures on the Elementary Psychology of Feeling and Attention* first published 1908 (New York: Macmillan); reprinted 1973 (New York: Arno Press)]? We overtly manipulated attentional allocation in three experiments to address the following questions: Is the flash-lag effect affected when attention is (a) focused on a single event in the presence of multiple events, (b) distributed over multiple events, and (c) diverted from the flashed object? To address the first two questions, five rings, moving along a circular path, were presented while observers attentively tracked one or multiple rings under four conditions: the ring in which the disk was flashed was (i) known or (ii) unknown (randomly selected from the set of five); location of the flashed disk was (i) known or (ii) unknown (randomly selected from ten locations). The third question was investigated by using two moving objects in a cost–benefit cueing paradigm. An arrow cued, with 70% or 80% validity, the position of the flashed object. Observers performed two tasks: (a) reacted as quickly as possible to flash onset; (b) reported the flash-lag effect. We obtained a significant and unaltered flash-lag effect under all the attentional conditions we employed. Furthermore, though reaction times were significantly shorter for validly cued flashes, the flash-lag effect remained uninfluenced by cue validity, indicating that quicker responses to validly cued locations may be due to the shortening of post-perceptual delays in motor responses rather than the perceptual facilitation. We conclude that the computations that give rise to the flash-lag effect are independent of attentional deployment.

1 Introduction

Visual perception is not instantaneous. Transmission of information from photoreceptors in the retina to ‘higher’ visual areas in the brain, on the one hand, and the abstracting properties of visual cortical neurons, on the other, can take significant amounts of time. Such a processing architecture introduces a temporal lag between the arrival of information at the receptors and perception. De Valois and De Valois (1991) have aptly described our visual experience as, “What we see, [], is not the world as it is now but as it was in the near past” (page 1625). One rather stark consequence of these neural delays is that the cortical representation of moving objects would be delayed. Thus, moving objects ought to appear spatially lagged. Consider an observer attempting to safely cross a railway line. Given an estimated delay of 100 ms (De Valois and De Valois 1991) a train traveling at 40 km h⁻¹ would appear 1.1 m behind its current location. The catastrophic consequence of such a misperception would be quite conspicuous.

2 The flash-lag phenomenon

Perceived spatial lags in the registration of visual stimuli have been observed in various perceptual settings. Mach (1897) noted an interesting effect based on saccadic eye movements. If the observer was surprised by a flash (spark), produced by a mechanical device, while making a saccade, the flash appeared displaced in the direction of pursuit relative to the device (page 61). MacKay (1958) had observers view a radio tube and move one eye by applying a gentle sideways pressure with the index finger. This passive

eye movement led observers to report a “violent perceptual disturbance” in which the glowing filament of the moving radio tube appeared to “jump out” of its briefly illuminated casing.

Strong mislocalization effects have also been observed when the eyes are held steady in the presence of a combination of moving and static stimuli. For example, Metzger (1932; in Mateeff and Hohnsbein 1988) reported that flashes of light were mislocalized when the background moved while the observer held steady fixation. Nijhawan (1994) presented observers with two types of events: a constantly visible line segment in continuous (real motion generated with analogue displays) rotary motion, and two line segments flashed in perfect spatial alignment with each end of the rotating one. The three segments were in fact parts of the same physical line in which the inner rotating segment was continuously visible and the two outer segments were flashed [see Wardle (1998) for a simple method for creating this demonstration]. The observer fixated the center of rotation. In this case, the flashed segments appeared to spatially lag the moving segment, producing a striking visual percept of a line broken into three pieces. This ‘flash-lag’ effect, as termed by Nijhawan (1994), scales as a function of velocity of the moving segment (Mateeff et al 1991; Nijhawan 1994; Wardle 1998) and even prevents color mixing when the flashed stimulus is a red line superimposed on a moving green bar (Nijhawan 1997).

Finally, mislocalizations have been reported in the presence of active, pursuit eye movements. In these experiments the eyes are set in motion during which a stimulus is briefly illuminated (Matin and Pearce 1965; Mateeff and Hohnsbein 1988; Nijhawan and Thornton 1996). Nijhawan et al (1998) instructed observers to track a dot moving from left to right in the presence of a continuously illuminated stationary green line. When the tracked dot was just below the green line, two red vertical lines were briefly flashed: one above the dot superimposed on the continuous green line and the other directly below the dot. Observers reported that both flashed lines were shifted rightward in the direction of pursuit relative to the continuous line. Furthermore, the upper flashed red line that was superimposed on the continuous green line did not mix with it to yield ‘yellow’, but rather appeared ‘red’. Thus, the flash-lag effect is rather robust in that it occurs in the presence of object motion and both passive and active eye movements.

3 Two accounts of the flash-lag effect

Multiple accounts of the flash-lag effect have been forwarded, such as visible persistence (Mach 1897; Nijhawan 1992; Kerkelberg and Lappe 2000), informational content (MacKay 1958), motion extrapolation and delay (Nijhawan 1994, 1997; Khurana and Nijhawan 1995; Nijhawan and Khurana, in press), attentional delay (Baldo and Klein 1995), differential visual latencies (Purushothaman et al 1998; Whitney and Murakami 1998; Whitney et al 2000), and most recently, postdiction (Eagleman and Sejnowski 2000). We shall outline the extrapolation-and-delay account and the attentional account in detail to provide the motivation behind the present experiments and reserve discussion of the other accounts until after the presentation of the results.

3.1 *Extrapolation-and-delay account*

Given significant transit delays of neural signals between the photoreceptors and higher cortical areas in the primate visual system, the retinal image location of a moving object should lead the object’s neural representation in higher, retinotopically organized, cortical areas. An ‘early’ visual operation, computationally akin to extrapolation, has been suggested to correct the cortical lag and maintain position correspondence between different processing levels for predictably moving objects (Nijhawan 1994, 1997; Khurana and Nijhawan 1995; Nijhawan and Khurana, in press). Consequently, the retinotopic site in the cortex maximally activated by a moving object will be the same as that activated

by a stationary object located where the moving object is at any given instant in time. A brief flash differs from a moving one in that it is unpredictable and, following transduction, the nerve signals triggered by the flash culminate in its perception after the expected delay. Thus, a flashed and a moving object in physical alignment can stimulate separate retinotopic cortical locations, with the moving object leading the flashed one. We shall refer to this view as the extrapolation-and-delay account of the flash-lag effect.

3.2 *Attentional account*

The extrapolation-and-delay account of the flash-lag effect has been questioned by Baldo and Klein (1995), who argued that the perceived lag of a flashed object relative to a moving one is the consequence of the delayed allocation of attention to the flashed object. Though not explicitly stated, this view must assume that moving objects solicit and sustain attentional deployment (Pylyshyn 1989, 1994) prior to the onset of the flashed object. Time delays then are a function of either attentional 'capture' by the flashed object in a stimulus-driven manner (Yantis and Jonides 1984, 1990; Nakayama and Mackeben 1989; Hillstrom and Yantis 1994; Yantis and Hillstrom 1994; Jonides and Yantis 1998), or attentional 'shifts' from the moving to the flashed locations (Tsal 1983; Weichselgartner and Sperling 1987; Watanabe and Shimojo 1998). On this view, the flash-lag effect is due to some time-dependent processes such as delays in visual attention which increase as a function of eccentricity (Tsal 1983; Baldo and Klein 1995; but see Nakayama and Mackeben 1989). These attentional processes act to bring the flashed object to a sufficiently high level of visual awareness, one that is presumably already achieved by the moving objects. Consequently, by the time the flashed object is fully registered, the moving objects have traversed some distance and thus the flashed object is incorrectly perceived to spatially lag the moving objects. The main support for this hypothesis stems from the observation that the magnitude of the flash-lag effect increases as a function of the spatial separation between the moving and flashed objects (Baldo and Klein 1995).

This attention-based modulation of the registration of flashed objects is similar to previous suggestions of attentional facilitation of the uptake of perceptual information. Consider Titchener's notion of prior entry. Titchener (1908/1973) presented observers with two simultaneously flashed lights and asked them to attend to one or the other. Observers reported a percept of the attended light appearing to come on before the unattended one. A similar account is given of the illusory line-motion phenomenon reported by Hikosaka et al (1993a, 1993b) in which a horizontal line, when presented in its entirety at one instant in time, appears to be drawn from the spatial location where the observer's attention was beckoned by the brightening of a dot. Thus the illusory line-motion results from a gradient of attentional facilitation that radiates in all directions from the cued location and weakens with distance (LaBerge 1983; LaBerge and Brown 1989; McCormick and Klein 1990; Stelmach and Herdman 1991; Stelmach et al 1994; Schmidt et al 1998; but see Downing and Treisman 1997).

Khurana and Nijhawan (1995) tested such an attentional account by exploring both the spatial and temporal delays posited by the 'attention shift' hypothesis. They presented observers with a display in which flashed and moving elements were spatially interleaved. Observers attentively tracked (Cavanagh 1992) a rotating line composed of six rectangles, and a horizontal line composed of six circles was flashed for 5 ms. As the flashed elements occupied the spaces between the attended rotating elements, it was argued that spatial attention shifts should be negligible and the flashed elements should appear not to lag. However, this display produced a strong flash-lag effect. Delays due to 'attention capture' were tested by the abrupt and simultaneous onset of both the flashed and moving elements for 5 ms and 1100 ms, respectively. In this 'flash-initiated' cycle the moving and flashed elements had an equally abrupt onset and therefore should have captured attention equivalently. A robust effect was measured that did not

differ significantly in strength from that observed in the 'complete' cycle. In sum, when flashed and moving objects are equated in terms of the shift-time or capture-time of attention, observers continue to report the flash-lag effect.

One could, however, argue that visual attention was not manipulated in the preceding experiments (Baldo and Klein 1995; Khurana and Nijhawan 1995), but rather it was implicitly assumed that moving objects are visually attended and that flashed objects capture attention by their abrupt onset. Also, the sparseness of the displays may not have sufficiently taxed attentional resources. In the following experiments, we explicitly directed observers' attention by providing advance information about upcoming events in displays of multiple objects. Furthermore, using a cueing paradigm (Posner 1980), we directed observers to either allocate their attention to a location where a flash was subsequently presented, or divert attention away from it. Such manipulations have a well-documented effect on the observer's reaction time to the flash, and provide a measure of attentional modulation. We used such a cueing procedure to ascertain the impact of attentional delays on the flash-lag effect. More specifically, does the magnitude of the flash-lag effect change as a consequence of cueing, ie do observers' reaction times to the flash co-vary with the flash-lag effect?

4 Experiment 1: Flash-lag effect and the spatial distribution of attention

We set about to address the following questions:

Is the magnitude of the flash-lag effect modulated when attention is distributed over multiple (i) potential flash sites and (ii) moving objects?

In order to do so, we devised a display with multiple moving objects. We began with a single object display that is known to produce a compelling flash-lag effect. While the observer fixates a dot on a middle-gray background, a black annulus moves along a circular path and a white disk is flashed in the center of the annulus (see figure 1). The white disk appears to spatially lag, and as a consequence 'fill' the annulus only partially (Nijhawan, submitted). The single ring-disk display was modified to a multiple-ring display in which five equally spaced rings rotated along a circular path (figure 1). Observers fixated the central fixation point and attentively tracked one or multiple rings under four different conditions.

4.1 Method

4.1.1 Observers. Two observers participated in the experiments. BK (an author) was cognizant of the hypothesis, while SP, though an experienced psychophysical observer, was naïve as to the hypothesis being tested. Both observers had normal or corrected-to-normal vision.

4.1.2 Apparatus and stimuli. The ring stimuli were mechanically rotated by a DC motor connected to a speed controller. The rings were mounted on a motorized rotary table (positioned vertically) connected directly to the motor shaft with a motor coupling. A metallic attachment to the motor shaft triggered the closure of a magnetic sensor switch which, in turn, activated a variable time delay (resolution 0.1 ms). The time delay terminated in a flash (duration 3 μ s) generated by a Strobotac[®] stroboscope. A mirror-type beam splitter was used to present the flashed disk in the optical plane of the rings, while another beam splitter projected a third channel of a fixation point onto the same optical plane. The observer's head was positioned on a chin rest with her/his eyes at a viewing distance of 117 cm from the display. The flash of the disk was synchronized to occur in the center of the moving ring at 0.5 Hz. The intensity of the light emanating from various stimuli was controlled with a pair of cross-polarized filters. The ring and the disk were deemed physically aligned when they appeared visually aligned to the experimenter while a second stroboscope (General Radio), synchronized with the first stroboscope, illuminated the moving ring for 3 μ s at 0.5 Hz. This method of

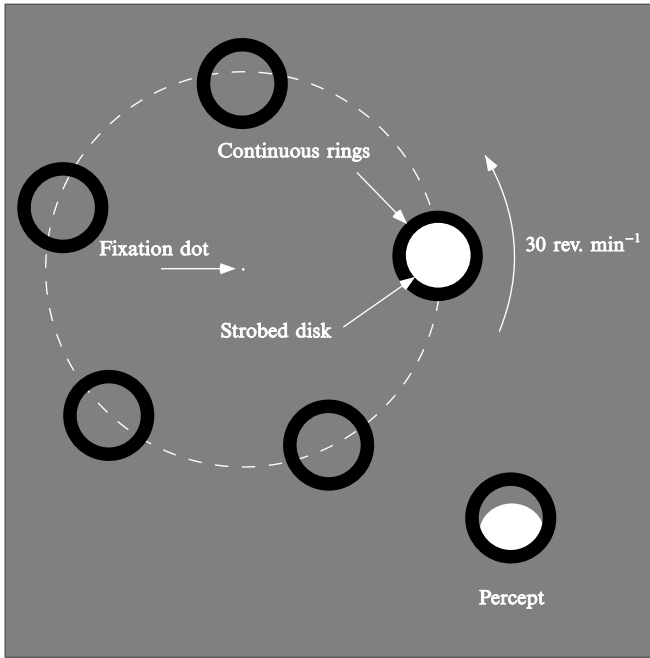


Figure 1. Multiple disk analogue display used in experiment 1. Observers fixated a central fixation point while the black rings rotated on a circular trajectory at a constant velocity of 30 rev. min^{-1} . A white disk was flashed coincident with the center of either a pre-cued or non-cued black ring when it occupied either a pre-specified or unspecified location in the trajectory. Observers reported perceiving the white disk trailing the black ring. A variant of this display in which only two rings 180° apart were presented was used in experiment 2.

aligning moving and stationary elements is quite accurate as confirmed by taking a photograph of the display with the camera shutter open. The alignment was periodically checked during the experimental trials to ensure that the disk was being presented in the center of a ring.

Diffusing material was used to provide uniform illumination for both the continuous and flashed stimuli. The luminance of the gray background was 8 cd m^{-2} . The black rings (luminance 0.0 cd m^{-2} , inner diameter 1.09 deg , outer diameter 1.40 deg) revolved on a circular path (instantaneous speed $13.66^\circ \text{ s}^{-1}$, path diameter 8.7 deg). The diameter of the disk was 1.09 deg . The disk was presented at one of ten positions along a circular trajectory, centered about the point of fixation. The alignment of the stimuli required not only precise timing but also precise relative positioning of the ring and the disk. Gross position adjustments were made with lab jacks and finer ones with a three-axis translation stage with 65 turns-per-inch screw adjustment.

4.1.3 Procedure. Although the experiment was performed in an entirely darkened laboratory, the observers remained light-adapted throughout the experiment by intermittent exposures to a light source. Observers viewed the display binocularly through natural pupils. They were told to foveate the fixation point and choose from a set of ten 'stills' the pattern that best matched their percept. Next to observer's left hand was a circular array which graphically depicted various spatial relations between the flashed disk and the ring. They ranged from the disk leading through the disk completely filling the ring to the disk lagging the ring (see *x*-axis of figure 2). The set of 'stills' was illuminated with an independent light source, switched on only when the observer was ready to make a selection. Observers rotated the circular array until the still that

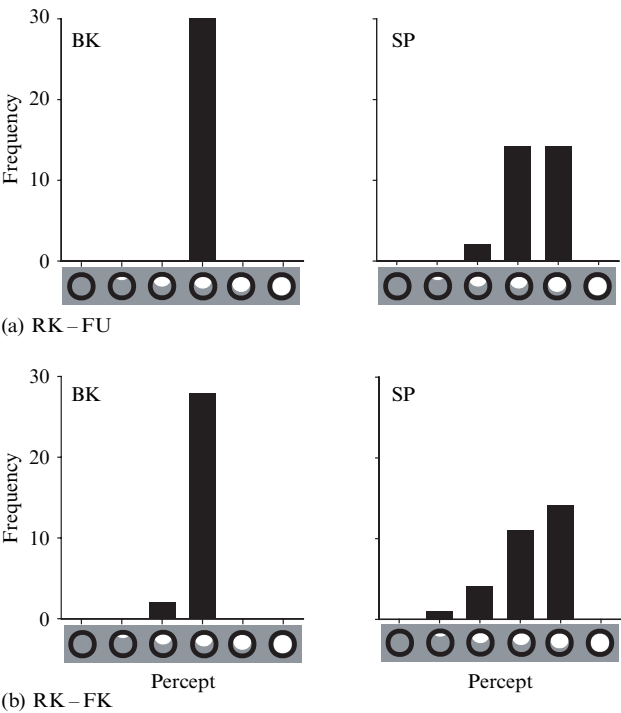


Figure 2. Results of experiment 1 — ring-known conditions. The horizontal axis shows the stills to which observers matched their percept. The vertical axis shows the frequency of each matched percept. (a) The magnitude of the flash-lag effect for two observers, BK and SP, when the ring was pre-cued but the location of the flashed disk was unknown (RK – FU condition). (b) The magnitude of the flash-lag effect for the same two observers when the location of the flashed disk was pre-specified (RK – FK condition).

matched their percept was in the location on the circular trajectory in which the disk was flashed. Each still was coded by numbers –4 to 4 representing the disk leading the ring in decreasing magnitude to the disk lagging the ring in increasing magnitude. The number 5 represented the disk completely filling the ring, and 0 signified no overlap between the center of the ring and the disk. Observer SP who was naïve as to the hypothesis was given verbal instructions regarding the task.

Each trial was initiated by a “ready” signal by the observer. The experimenter then presented the appropriate preview, if any, and then set the display into motion. Each trial ended with the flash of the disk, at which point the observer selected a match from the array of stills. The experimenter recorded the assigned number of the still and waited until the observer said “ready” to begin the next trial. Experiment 1 consisted of four conditions (described below) of thirty trials each. The order of the conditions was randomized over the two observers.

The deployment of attention to the moving ring(s) and the flashed disk location(s) was manipulated in accord with the 2 × 2 contingency table shown below.

RK – FK: Ring known and flash location known. Both the ring and flash location were

Flash location	Ring	
	known	unknown
Known	RK – FK	RU – FK
Unknown	RK – FU	RU – FU

specified at the beginning of the trial. The to-be-attentively-tracked ring was aligned in the 12 o'clock position at the beginning of each trial and the disk was pre-flashed in the location in which it would be later flashed during the trial. In this manner the observers

knew exactly in which ring and at which location the flash would occur. Observers fixated the central dot and attentively tracked the 12 o'clock ring when it started moving. *RK – FU: Ring known and flash location unknown.* The to-be-attentively-tracked ring was aligned in the 12 o'clock position at the beginning of each trial. The rings were set into motion and the flash subsequently occurred in any one of ten randomly sampled locations in the circular trajectory. Thus, though the observers did not know the location of the flash, adequate tracking of the ring would ensure their attention to be fully present when the disk was indeed flashed (Khurana and Nijhawan 1995). *RU – FK: Ring unknown and flash location known.* The observer was presented a preview of the location in which the disk would be flashed at the beginning of the trial. In this condition the ring in which the disk was to be flashed was not known to the observer. *RU – FU: Ring unknown and flash location unknown.* Observers were instructed to distribute their attention to all the rings and the entire circular trajectory. Both the ring in which the disk was to be flashed and the flashed disk location were unknown to the observer. They were chosen randomly for each trial.

4.2 Results and discussion

The following 2 × 2 tables depict the predicted outcomes of the attentional versus extrapolation-and-delay hypotheses. FLE stands here for flash-lag effect.

Attentional account			Extrapolation-and-delay account		
Flash location	Ring		Flash location	Ring	
	known	unknown		known	unknown
Unknown	significant FLE	significant FLE	Unknown	significant FLE	significant FLE
Known	reduced FLE	reduced FLE	Known	reduced FLE	reduced FLE

Let us begin by analyzing the various conditions in terms of attentional deployment and their consequences for processing delays. Presumably the maximum flash-lag effect should be had when knowledge of the flash location is at a minimum. Conversely the flash-lag effect should be significantly reduced or not present when there is good advance knowledge of the flash location so as to permit the advance deployment of attention. On the other hand, one could posit a difficulty in maintaining attention at an empty spatial location in the presence of moving stimuli (Khurana and Kowler 1987), hence all the tests of cues on the flash-lag effect were two-tailed.⁽¹⁾ The critical differences between the two accounts are the predictions made for the conditions in which the flash location is known versus those in which it is unknown at the beginning of a trial. According to the attentional account the differences in the observed flash-lag effect between the known versus unknown conditions should be significant while according to the extrapolation-and-delay account there should be no differences as attention cannot impact the transmission delays.

All in all, there was no significant modulation of the flash-lag effect over the four conditions. Let us first consider the ring-known conditions: The ring was specified to observers before the onset of an actual trial by aligning it with the 12 o'clock position. In order to maintain its identity throughout the trial observers were instructed to attentively track it. Both observers found the task relatively easy and never reported losing track of the designated ring. Figure 2 depicts a distribution of stills chosen by observers BK and SP in these conditions. The ring-known flash-unknown (RK – FU)

⁽¹⁾ We thank an anonymous reviewer for pointing this out.

condition is the most similar to the basic flash-lag effect reported with other displays (Nijhawan 1994; Baldo and Klein 1995). A significant flash-lag effect was measured for both observers in this condition. Observer BK had a mean flash-lag effect (FLE) of 3.00 (t_{29} could not be computed owing to lack of variability) while observer SP showed a mean effect of 3.4 (t_{29} ; one-tailed = 14.10, $p < 0.001$; assuming a value of 5 as the percept of the physical stimulus in which the disk completely fills the ring). Note that neither observer ever reported seeing the disk fill the ring which was the physical state of affairs.

The RK – FK condition is the more focused attention condition because the observer's attention was completely focused on the critical event. Observer BK had a mean flash-lag effect of 2.93 (t_{29} ; one-tailed = 44.62, $p < 0.001$) and observer SP one of mean magnitude 3.27 (t_{29} ; one-tailed = 11.47, $p < 0.001$). The flash-lag effect in this focused attention condition did not change in magnitude from that reported in the RK – FU condition (BK: t_{29} ; paired, two-tailed = 1.44, $p > 0.05$; SP: t_{29} ; paired, two-tailed = 0.72, $p > 0.05$). These findings are in accord with the extrapolation-and-delay account but are difficult to reconcile with an attentional account. In the RK – FK condition the observers had full prior knowledge as to the ring in which, and where in the circular trajectory, the flash was to occur. Yet even with the complete deployment of attentional resources a significant flash-lag effect was observed.

When neither the ring in which the disk was to be flashed nor the location of the disk flash was known to the observer (RU – FU condition), a significant flash-lag effect (see figure 3) was measured for both observers (BK: FLE = 2.93; t_{29} ; one-tailed = 44.62, $p < 0.001$; SP: FLE = 3.10; t_{29} ; one-tailed = 15.73, $p < 0.001$). Even when the location of the flashed disk was made known to the observer at the beginning of the trial, observers reported perceiving the disk to lag the ring (BK: FLE = 2.73; t_{29} ; one-tailed = 27.60, $p < 0.001$; SP: FLE = 3.37; t_{29} ; one-tailed = 10.52, $p < 0.001$). Once again, advance knowledge of the flash location did not reflect in the magnitude of the flash-lag effect

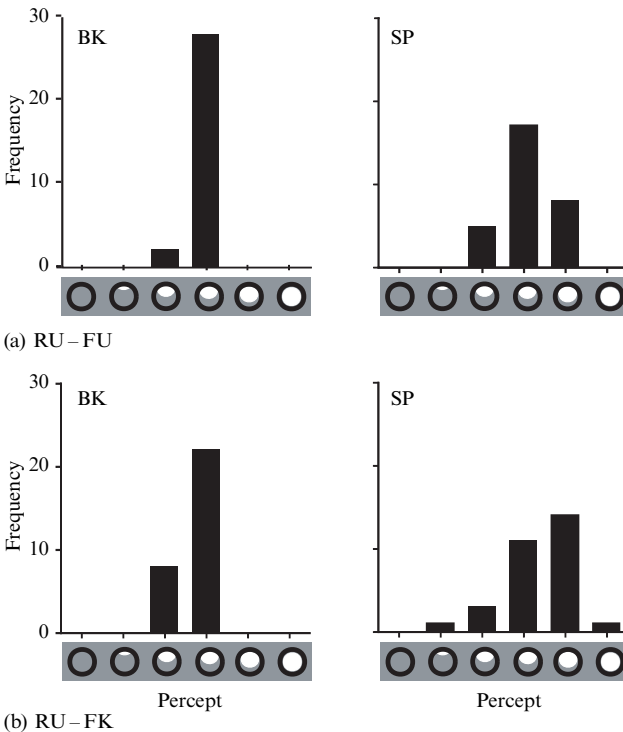


Figure 3. Results of experiment 1—ring-unknown conditions. (a) The magnitude of the flash-lag effect for observers BK and SP, when neither the ring or the disk location was known in advance (RU – FU condition). (b) The perceived flash-lag effect when the ring was non-cued but the location of the flashed disk was pre-specified (RU – FK condition).

for either observer (BK: t_{29} , paired, two-tailed = 1.99, $p > 0.05$; SP: t_{29} , paired, two-tailed = 1.44, $p > 0.05$). It is interesting to note that there was a small (7%) reduction in the flash-lag effect for observer BK and a comparable (9%) increase for observer SP. Hence there was neither a significant nor consistent change in the flash-lag effect as a function of advance knowledge of flash location. In sum, regardless of whether the moving or flashed objects were viewed with focused or divided attention, the magnitude of the spatial lag of the disk relative to the ring remained largely unaffected.

5 Experiment 2: Flash-lag effect and the spatial cueing of attention

Though we found the flash-lag effect to be unchanged by the distribution of attention over the visual array, it certainly could be influenced by diverting attention from the flash itself. In other words, does the flash-lag effect occur when attention is diverted from the site of the flash? In order to investigate this hypothesis we employed a cost–benefit cueing procedure (Posner 1980). A new display was created in which there were two rings, located 180° from each other, revolving on a circular path.

5.1 Method

5.1.1 Observers. The same two observers that participated in experiment 1 took part in experiment 2.

5.1.2 Apparatus, stimuli, and procedure. Aside from the configuration of the rings, other stimulus parameters and procedures were identical to those in experiment 1. Experiment 2, however, consisted of two sessions.

5.1.3 Session 1: Cue-and-flash-consistent trials. On 70% of the trials ($n = 35$) an arrow cue that pointed to either the 3 or 9 o'clock position was presented 100 ms prior to the flash. The disk was then flashed at either the 3 or 9 o'clock position. The location of the flashed disk was consistent with the direction of the arrow.

5.1.4 Session 1: Cue-and-flash-inconsistent trials. On the remaining 30% ($n = 15$) of the trials, when the arrow cue (presented 100 ms prior to the flash) pointed to the 3 o'clock position, the disk was flashed at the 9 o'clock position, and vice-versa. These trials were randomly interleaved with the cue-and-flash-consistent trials.

5.1.5 Session 2: Uninformative-cue trials. On 100% of the trials ($n = 50$) a double-sided arrow that pointed to both the 3 and 9 o'clock position was presented 100 ms prior to the flash. The white disk was then randomly flashed in either the 3 or 9 o'clock position.

5.2 Results and discussion

Figures 4 and 5 show the data for the two observers. For uninformative-cue condition a significant flash-lag effect was obtained for both observers (BK: FLE = 2.96, t_{49} , one-tailed = 72.87, $p < 0.001$; SP: FLE = 3.6, t_{49} , one-tailed = 20.0, $p < 0.001$). When the arrow cue was consistent with the location of the flash there were no benefits of attentional deployment, as the effect remained similar to that in the uninformative-cue condition for both observers (BK: FLE = 2.97, t_{34} , one-tailed = 71, $p < 0.001$; SP: 3.51, t_{34} , one-tailed = 15.64, $p < 0.001$).

Most interestingly, the flash-lag effect in the cue-and-flash-inconsistent condition showed no increase in the effect due to attention being drawn away from the flash site. For observer BK the mean magnitude of the effect was 2.97 (significance could not be computed owing to lack of variability). For observer SP the mean magnitude of the effect was 3.4 (t_{14} , one-tailed = 7.48, $p < 0.001$). Neither observer's perception of the flashed disk relative to the moving ring was altered as a function of cueing.

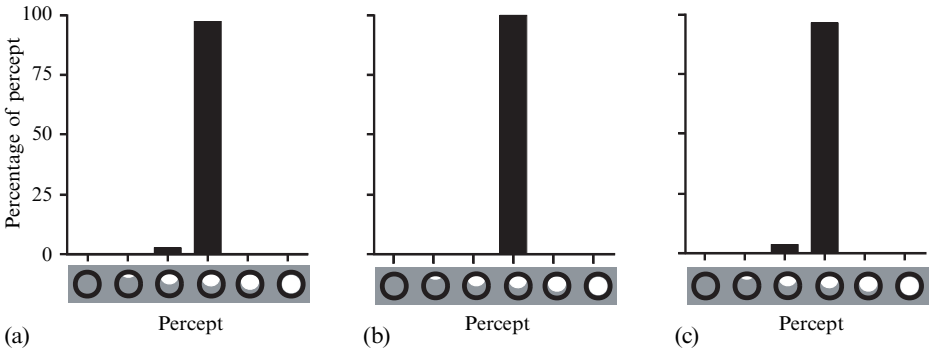


Figure 4. Results of experiment 2—observer BK. The horizontal axis shows the various stills to which BK matched her percept. The vertical axis shows the percentage of each percept. (a) The condition in which the advance cue and the location of the flash were consistent. (b) The condition in which the cued location and the flashed-disk location were inconsistent. (c) The flash-lag effect when an uninformative cue was presented.

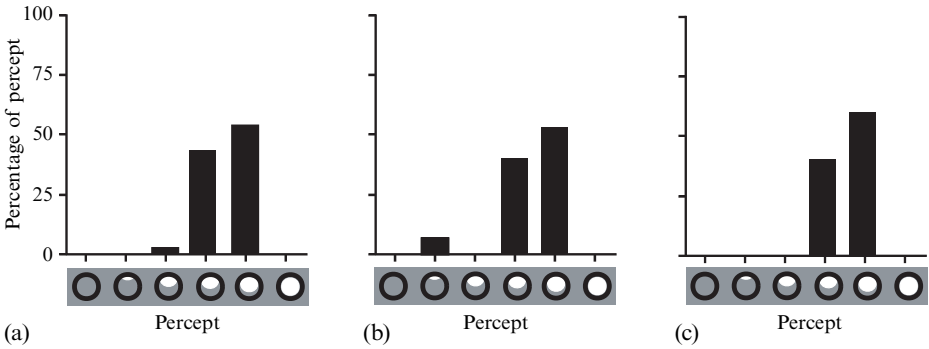


Figure 5. Results of experiment 2—observer SP. See figure legend 4 for details.

6 Experiment 3: Flash-lag effect and the modulation of attention

One may argue that the previous experiments did not employ an independent measure of attentional cueing and therefore one cannot assess how effectively attention was manipulated. For example, if observers did not attentively track well in experiment 1, the lack of difference in the known versus unknown conditions becomes uninformative. In experiment 2 no measure of cue validity was taken, thereby limiting the interpretation of the data. Additionally, the sparseness of the displays may have rendered the inconsistent and consistent conditions equivalent to the uninformative condition. It may also be suggested that the measure of the flash-lag effect employed in the above experiments is too coarse to pick fine differences in perception as a function of attentional modulation. Finally, these results are not directly comparable to the Baldo and Klein (1995) findings because of their use of analogue displays. Experiment 3 was designed to overcome these concerns.

In order to make the experimental displays more similar to those used by Baldo and Klein (1995) we presented the stimuli on a CRT display (controlled by a PowerMac). Once again, a cost–benefit cueing procedure was used. Observers were presented two black lines moving horizontally from left to right on a gray background. An arrow (80% valid) indicated the location of an upcoming flash of a horizontal white line adjacent to one of the moving lines (see figure 6). The horizontal offset of the flashed white line relative to the moving black line was varied randomly from trial to trial (method of constant stimuli). Observers were asked to perform two tasks. First, they were to indicate by pressing one of two keys, as quickly as possible, the location of

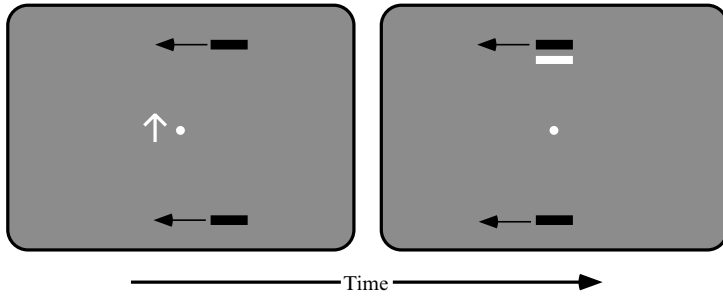


Figure 6. Stimulus configuration for experiment 3. Observers viewed two black lines move from right to left while fixating the central dot. 500 ms prior to the flashed white line an arrow cue was presented for 333 ms that was valid in terms of flash location on 80% of the trials and invalid on the remaining 20% of trials. Observers were required to press a key indicating the location of the flashed white line as quickly as possible and also whether it appeared to lag or lead the adjacent black line. The flashed white line was offset from the black line in 2 min of arc steps ranging from 0 (completely aligned) to 14 min of arc (significantly leading).

the flashed line. Second, they were to report whether the flashed line appeared ahead of or behind the moving line, in a two-alternative forced-choice procedure.

6.1 Method

6.1.1 Observers. Three new observers participated in experiment 3. The two authors, KW and RN, were psychophysically experienced and non-naïve, while MW was psychophysically inexperienced and was not aware of the hypothesis.

6.1.2 Apparatus and stimuli. Stimulus displays were generated and data collected with a Power Macintosh computer. The displays were presented on a screen ($38^\circ \times 29^\circ$) with a refresh rate of 60 Hz. Observers, seated 60 cm from the computer screen, viewed two horizontal black lines ($0.13^\circ \times 1.07^\circ$; 0.0 cd m^{-2}) moving leftward at 4° s^{-1} on a gray background (8.5 cd m^{-2}) traversing a total distance of 3° . One line was presented 1.8° deg above the fixation point ($0.13^\circ \times 0.13^\circ$) and the other 1.8° deg below it. On every trial an arrow cue was displayed for 333 ms. This arrow pointed either up or down and was presented 0.5° to the left of the fixation point, 500 ms prior to the flash. The flashed white line (94.5 cd m^{-2}) was presented 1.5° deg above or below the fixation point. On 80% of the trials the location of the flashed white line was consistent with the direction of the arrow (cue-and-flash-consistent condition). On the remaining 20% of the trials the location of the flashed white line was inconsistent with the direction of the arrow (cue-and-flash-inconsistent condition). Cue-and-flash-consistent and cue-and-flash-inconsistent trials were randomly combined.

6.1.3 Procedure. Observers indicated whether the flashed white line was presented above or below fixation by pressing the appropriate keys. This was a speeded task. They then went on to indicate whether the flashed line was to the left or right of the moving line by pressing two other keys. Each session consisted of 80 trials (in 8 out of every 10 trials the cue and flash were consistent and in 2 they were inconsistent). Eight different spatial arrangements were tested in which the flashed line was either aligned or ahead of the moving line in steps of 2 min of arc. Thus, the offset of the flashed white line relative to the moving lines ranged from 0 to 14 min of arc. For each offset, a total of 10 trials were presented (8 valid-cue trials, 4 above and 4 below fixation; 2 invalid-cue trials, 1 above and 1 below fixation in a single session). The entire experiment consisted of ten self-paced sessions.

6.2 Results and discussion

With all observers tested, valid cueing resulted in significantly faster responses ($p < 0.001$), verifying that attention was successfully manipulated (Posner 1980) (see figure 7a). This significant and robust difference in reaction time, however, did not translate into a significant difference in the flash-lag effect for any single observer. The difference in the perceived spatial lag of the flashed line (calculated as the point of subjective equality of the psychometric functions and averaged over three observers) was negligible (see figure 7b). Thus, although attention dramatically shortened the response time to the cued flash, showing that attention was successfully deployed to one spatial location or another based on the cue, it did not significantly impact the flash-lag effect.

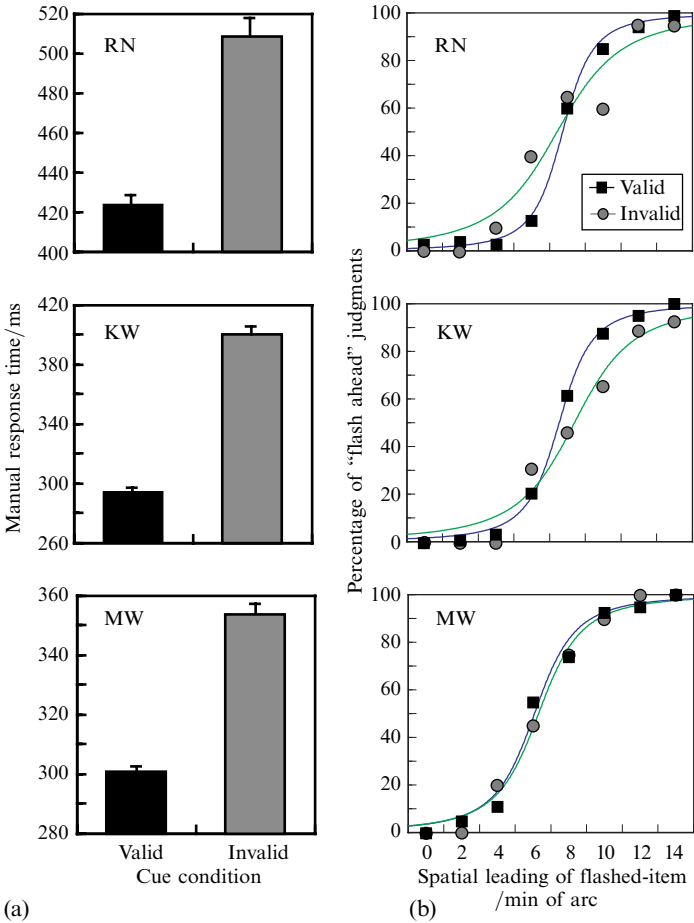


Figure 7. Results of experiment 3. (a) Response times for three observers to the flash location. The horizontal axis shows valid and invalid trials. Observer RN's mean reaction time was 424.1 ms for valid trials and 508.2 ms for invalid trials ($p < 0.001$). The other experienced and non-naïve observer, KW, indicated the location of the flash in 295 ms on valid trials while taking 399.9 ms on the invalid trials ($p < 0.001$). Similar results were obtained for the inexperienced naïve observer MW, who took on average 300.7 ms to respond on valid trials and 353.4 ms on invalid ones ($p < 0.001$). (b) Psychometric functions to the perceived alignment of the flashed white line relative to the black moving line. Valid trials are shown in black and invalid trials are shown in gray. The percentage of times the observer perceived the flashed line to be ahead of the moving line is plotted against the physical offset of the flashed line.

The question of how attention affects perception has always been a complicated one (James 1890; Kowler 1994). For instance, attentionally mediated improvements in performance can result from enhanced perceptual processing, differential capacity allocation, or internal noise reduction (Lu and Doshier 1998). In terms of enhanced visual processing, it has been suggested that attending to a spatial location facilitates processing of stimulus information at that site (Titchener 1908/1973; Posner and Petersen 1990; Hikosaka et al 1993a, 1993b; Desimone et al 1994; Shimojo et al 1995). Though the Posner (1980) cueing paradigm investigates what might be considered post-perceptual contributions to visual processing, such as the effects of expectation of a signal at a given location, cueing is generally characterized as leading to signal enhancement. In previous cueing experiments, response time has been the primary measure available to gauge enhanced performance. Change in response time with modulation of attention could, in the absence of other performance measures, be attributed to facilitation anywhere along the visuomotor pathways activated prior to the response. Thus, shorter reaction times to cued locations could result from either perceptual or post-perceptual facilitation. The flash-lag phenomenon permits a measure of the contribution of visual delays to response time. In the present experiments employing the flash-lag effect, we find a clear and robust dissociation between motor response time and perception. Thus, the lack of modulation of the flash-lag effect found here suggests that cueing primarily facilitated post-perceptual processes. Furthermore, it may be that in general the attentional quickening of response times in cost–benefit cueing experiments is indeed attributable to post-perceptual processes (Shaw 1984; Sperling and Doshier 1986; Kinchla 1992). In sum, differential allocation of attention to flashed locations can cause the shortening of a motor response to the flashed location without speeding up the actual processing of location information. Thus, attentional modulation, as an explanation of the flash-lag effect, is untenable (Khurana and Nijhawan 1995).

7 Other accounts of the flash-lag effect

In the interest of completeness, we examine several other accounts of the flash-lag effect and the relevant empirical evidence.

7.1 *Visible persistence*

Mach (1897), who may have been the first to report mislocalization of a flash relative to a continuously visible object, suggested that the effect was due to visible persistence of the flash. This account was rediscovered by Nijhawan (1992) and has been significantly extended by Krekelberg and Lappe (2000). However, the account, contrary to observers' reports, predicts that the flash should abut the moving item at the beginning of the persistence period (say 100 ms), and the flash-lag effect should appear toward the end of this period (Nijhawan 1994; Cavanagh 1997). Additionally, if the persistence of the flash is reduced by a masking stimulus, both the flash-lag effect and the resulting color-decomposition effect occur undiminished (Nijhawan 1997; Whitney et al 2000).

7.2 *Differential visual latencies*

Metzger (1932, in Mateeff and Hohnsbein 1988) suggested that the lag of a flash was due to differential visual latencies of the moving versus the flashed items. Recently, Purushothaman et al (1998) manipulated the luminance of the moving and the flashed items relative to the background and found that the flash-lag effect decreased with increased contrast of the flash, and decreased contrast of the moving item relative to the background. Taking a different approach, Whitney and Murakami (1998) showed that a moving object does not appear to overshoot the point where it abruptly reverses direction at the moment of a flash (Whitney et al 2000). These observations have been taken as evidence for the existence of differential processing delays between moving versus flashed items. We have tested this account separately using reaction-time measures

and temporal-order judgments and have failed to find *prima facie* evidence for it (Nijhawan et al, submitted).

7.3 Informational content

MacKay (1958) suggested that the mislocalization effect was due to the dramatically different information content of the continuously illuminated (moving on the retina owing to externally forced eye movements) and flashed items. Change requires informational support, while lack of change requires relatively little informational support. A flash is informationally weak so the visual system treats it as unchanging and stationary, while an informationally rich, continuously visible stimulus is perceived to change position when the eyeball is forced to move by gentle pressure of the finger (see section 2). In this manner, a flash will appear to be mislocalized relative to a continuously visible item. This account also predicts an initial no-lag percept and a separation between the two items to appear when the item moved by finger pressure has arrived at its final position. However, the report of observers could not be more different [the flashed item appears in a lagging position relative to the continuously visible item when the flash is first registered (Nijhawan 1994)].

7.4 Postdiction account

Most recently, Eagleman and Sejnowski (2000) proposed a ‘postdiction’ model of the flash-lag effect. They employed a ‘flash-terminated’ cycle (initially referred to as ‘past-interval’, see Nijhawan 1992). This cycle complements the ‘flash-initiated’ cycle (Khurana and Nijhawan 1995) (initially referred to as ‘future-interval’, see Nijhawan 1992), and consists of events only up to the flash. Note that the ‘flash-terminated’ and the ‘flash-initiated’ cycles together form the standard ‘complete’ cycle display (figure 8a).

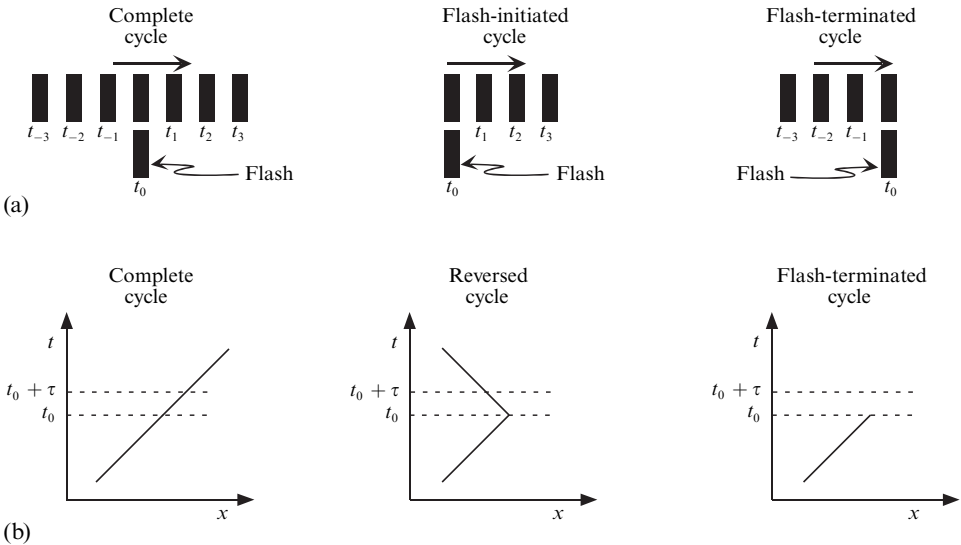


Figure 8. (a) Schematic representation of three different cycles used to investigate the flash-lag effect (see Nijhawan 1992). In the complete cycle the moving object is visible both prior to and after the flash. In the flash-initiated cycle the moving object is invisible before the flash, but is visible afterwards. In the flash-terminated cycle, the moving object is visible prior to the flash, but is invisible afterwards. (b) Time–space plots of three different trajectories of the moving item (solid line) in the complete, reversed, and flash-terminated cycles. A delay of τ ms is assumed between the physical flash (occurring at t_0) and its perception (occurring at $t_0 + \tau$). Note that in the reversed cycle, the motion depicted after t_0 is identical to that in the flash-initiated cycle [see (a)], but opposite in direction. Also, note the difference in the trajectory of the moving item between t_0 and $t_0 + \tau$ (dashed lines) for the three conditions.

Eagleman and Sejnowski (2000) contrasted a prediction model (extrapolation) that suggests that the past trajectory of a moving item influences its position relative to a flash, with a postdiction model that holds that the trajectory of a moving object after the flash influences its position relative to the flash. They presented observers with identical trajectories of the moving item prior to the flash, but, after the flash, the moving item either (i) continued on its trajectory (complete cycle), (ii) reversed direction (reversed cycle), or (iii) stopped (flash-terminated cycle). Since the past events in the three conditions were identical, according to them the extrapolation model should predict no difference between the three conditions (see figure 8b). However, the 'flash-terminated' cycle did not produce a flash-lag effect, consistent with the findings of Nijhawan (1992), while reversal of direction produced an effect equal to that observed in the 'complete' cycle and the 'flash-initiated' cycle. Thus, Eagleman and Sejnowski (2000) concluded that the critical motion trajectory is that occurring after the flash.

However, the critical question here is: Which time marker, the time of the physical flash or the time at which it is perceived, is to be used to define what occurs in the past and what in the future? If one considers the trajectory of the moving item prior to the perception of the flash, which, owing to transmission delays, occurs τ ms (~ 100 ms) after the physical flash, then, contrary to the postdiction account, the trajectory of the moving item in the three conditions outlined above is not identical. For example, in the 'flash-terminated' case the moving item is stationary on the retina for the τ ms period following the physical flash, which is not the case for the other two conditions (see figure 8b). Clearly, the trajectory of the moving item in this τ ms period contributes to the final percept.

Thus, while the present findings pose substantial difficulty for an attentional account they do not directly address the other accounts discussed above. We maintain that motion extrapolation remains an effectual explanation based on a minimum number of independent assumptions. Furthermore, at present it is the only account with direct physiological support. Evidence for some form of extrapolation has been reported in the retina of the salamander and rabbit (Berry et al 1999). However, it is unclear whether (a) the same would hold true for the primate retina given that primate ganglion cells are not directionally selective (Hubel and Wiesel 1968; Gegenfurtner 1999) and (b) retinal compensation is adequate for delays in further processing. Extrapolation, compensating for neural delays, in the cortex could be achieved by neurons that demonstrate 'predictive remapping'. For these neurons, the latency for a target with an abrupt onset in a cell's receptive field is greater than the response latency for a target entering the cell's receptive field from some other location (Duhamel et al 1992). Thus, at a single instant in time, two sets of active cells of this type—one activated by a moving object and the other by a retinally aligned flash—would code nonoverlapping retinotopic locations.

8 Conclusions

The flash-lag effect is not affected by attentional deployment. First, we show that direct manipulations of attentional resources neither decrease nor increase the flash-lag effect. Second, an attentional mechanism would probably be too high-level to produce the spurious edges which accompany the flash-lag effect in experiments 1 and 2 (Watanabe et al 1999; Nijhawan, submitted; Watanabe et al, submitted), or the color decomposition effect (Nijhawan 1997; Nijhawan et al 1998). In accord with such a suggestion Khurana et al (1999), using a visual search task, showed that the spurious edges produced by the flash-lag effect are available to pre-attentive vision.

The present findings imply that both the 'lag-correction' of moving objects and the registration of flashed objects are due to neuronal transmission delays rather than attentional delays. Thus, the spatial correction for moving items is completed prior to atten-

tional processing and visual awareness (Treisman 1993). Such a proposal is consistent with previous suggestions that the visual system has a certain minimum time interval within which the presence of a new object is registered (Yantis and Hillstrom 1994) or a new 'object file' is set up (Duncan 1984; Kahneman et al 1992; Kanwisher and Driver 1992).

Finally, the dissociation between the perceived location of a flash and the time taken to respond to it indicates that the response advantage to an attended site based on cue validity may not be due to enhanced perceptual processing. Indeed, the perceptual phenomenon of the flash-lag effect provides a powerful tool in assessing the visual component of visuomotor latencies.

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